# Role of disturbance, geology and other environmental factors in determining abundance and diversity in coastal avian communities during winter

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ABSTRACT: Wading birds are important predators in intertidal communities. Their ecology and distribution have been widely studied in estuarine wetlands, but little is known about the factors determining their abundance and diversity in the more common non-estuarine coasts. We analysed data from a large-scale survey of wader (Charadrii) populations in the non-estuarine coasts of Portugal (length = 1096 km), during winter, together with variables related to disturbance, habitat and geophysical characteristics of the coast to explain the patterns of wader abundance and diversity. The wintering community is composed of 13 species and dominated by ruddy turnstones *Arenaria interpres* and sanderlings *Calidris alba*. Wader abundance was limited by direct disturbance from humans and the presence of peregrine falcons *Falco peregrinus*. Overall human presence, availability of rocky intertidal areas, presence of nearby estuarine wetlands and low winter temperatures favoured higher wader densities. Areas dominated by igneous and metamorphic rocks (basalts, granites, schists and greywackes, and diabases) harboured a more diverse wader community than areas with sedimentary rocks or with sandy beaches, suggesting that coastal geology may have a structuring role for wader communities, which had not yet been described. Understanding these patterns gives useful directions as to where one should focus conservation efforts in non-estuarine coastal areas.

KEY WORDS:  Distribution · Geophysical variables · Human disturbance · Intertidal community · Non-estuarine coastline · Rocky shore · Wader

## INTRODUCTION

Intertidal habitats are among the most productive in the world (Costanza et al. 1997), having a highly specialized community of species adapted to the unstable nature of these environments governed by tidal cycles (Raffaelli & Hawkins 1996). Intertidal communities are regulated not only by tidal regimes but also by a number of other factors, namely substrate type (McQuaid & Branch 1984), level of exposure to waves (McQuaid & Branch 1984, Bustamante & Branch 1996) and the biological interactions between different species (Woodin 1974).

Upper trophic level predators, such as birds, fishes and mammals, can have a profound effect on these communities, regulating the abundance and diversity of species lower on the food chain (Estes & Duggins 1995, Ellis et al. 2007). Their distribution and behaviour is also dependent on the abundance and availability of their prey and, consequently, on the various factors influencing prey distribution.

Waders (Aves: Charadrii) are important predators in many intertidal communities (Wootton 1997, Rosa et al. 2008), especially during winter, when millions of these birds spread along the mid- and low-latitude coastlines of the world to find areas of favourable feeding conditions and amenable weather before migrating back to their high-latitude breeding grounds in the following spring (van de Kam et al. 2004). They tend to congregate in sheltered estuarine wetlands, where they forage in soft tidal flats during low tide. Most research on the ecology and distribution of waders has been focused on these sheltered environments, highlighting the importance of prey abundance and availability (Piersma et al. 1993), sediment characteristics (Mouritsen & Jensen 1992, Granadeiro et al. 2007, Kuwae et al. 2010), predation risk (van den Hout et al. 2008), human disturbance (Gill et al. 2001) and microhabitat characteristics (Lourenço et al. 2005).

Unlike estuarine tidal flats, non-estuarine coasts under tidal regimes are generally narrow and mostly composed of either rocky or coarse sandy substrates. Also, the open coast is much more exposed to waves, which may limit its availability for birds due to the frequent submersion of the intertidal during low tide but also creates a splash zone that will harbour intertidal invertebrates above the high tide line (Raffaelli & Hawkins 1996). These coastal areas often have a rich intertidal fauna and flora, providing favourable food resources for waders (Dierschke 1993, Wootton 1997). In fact, important numbers of several wader species are found in non-estuarine coastal areas during the winter (Burton at al. 2008). The few studies on the subject have identified factors such as substrate type (Lorenzo & Emmerson 1996, Summers et al. 2002), exposure to waves and intertidal width (Summers et al. 2002), and organic enrichment by human sewage (Burton et al. 2002) in determining wader distribution on non-estuarine coasts.

Understanding the distribution of waders on non-estuarine coasts involves much wider spatial scales than those observed within estuaries, so climatic variables such as rainfall and temperature may also be important (Rehfisch et al. 2004). Of course, the distribution and abundance of invertebrate prey are likely to mediate the relationship between most of these factors and the distribution of waders on non-estuarine coasts (Kendall et al. 2004), so any other factors that influence invertebrate distribution may also have an impact on waders.

Coastal geology is one such factor. Although, to our knowledge, no studies have explored the effect of coastal geology on wader communities, it is known to have an effect on the recruitment and mortality of invertebrates such as *Chthamalus* barnacles (Raimondi 1988, Herbert & Hawkins 2006), but no consistent effects on the density and survival of other species, such as the barnacle *Tesseropora rosea* (Caffey 1982). Also, the rock mineral composition seems to influence the structure of epibenthic sessile communities (Bavestrello et al. 2000). Friable and soft rocks such as limestones, chalks and sandstones may be unsuitable for larger invertebrates and plants, as they provide less secure anchorage than harder rocks (Lewis 1964). Harder rock types may provide more diverse microhabitats and better refuge from predators and physical disturbance due to their ruggedness (Barry & Dayton 1991, Walters & Wethey 1996) but will also be less favourable for animals that are able to burrow into softer rocks (Raffaelli & Hawkins 1996).

In this contribution, we used data from a large-scale survey of wader populations in the non-estuarine coasts of Portugal and related this information with several environmental variables to investigate the factors that (1) explain specific abundance and (2) structure wader communities in non-estuarine coastal areas.

## METHODS

### Study area

The full length of the non-estuarine coast of Portugal (excluding islands) was covered. This coast is rather diverse, including long stretches of sandy beaches, low rocky shores, steep cliffs with small pocket beaches and barrier islands, as well as fishing and recreational harbours and a few sections protected by seawalls. There are also several important estuarine areas on the Portuguese coast, which were not studied here. The tidal regime is semi-diurnal with amplitudes that vary between 2 and 4 m. The non-estuarine coast of Portugal harbours the majority of the national wintering populations of sanderling *Calidris alba* and ruddy turnstone *Arenaria interpres* and 10 to 35% of the national wintering populations

of whimbrel *Numenius phaeopus*, Kentish plover *Charadrius alexandrinus*, ringed plover *Charadrius hiaticula* and common sandpiper *Actitis hypoleucos* (M. Lecoq et al. unpubl. data).

The coast was divided into 198 Universal Transverse Mercator squares (5 × 5 km) (Fig. 1), but some squares included only a very small extension of coastline. These very small stretches could bias the analyses and were thus included in the immediately adjacent square. This resulted in a total 156 coastal sections. The length of the coastline, including all piers, jetties and sea walls, was measured to be 1096 km based on aerial imagery (the most recent coverage available in Google Earth) from an altitude of 1000 m. Of this total length, 1% represents the mouths of estuarine areas, which were excluded from this study.

### Bird surveys

All coastal sections were visited by experienced observers during the winter from 2009 to 2011. The vast majority of visits took place in the first winter

(from 5 December 2009 to 14 February 2010), with the remaining ca. 4% being done in the second winter (from 10 December 2010 to 23 February 2011). The observers walked the full length of coastline within their section of the coast, counting all waders that had either landed or taken flight during the count. Inaccessible areas, such as cliffs, rocky shoals or private piers, were counted from vantage points. Most sections (83%) were fully covered, while the remaining had coverages of 20 to 95%.

All counts took place for a period of ±3 h around low tide, when most intertidal areas are exposed, and only in days of favourable weather and sea conditions to ensure both the safety of the observers and good visibility. A few sectors with very high cliffs and poor visibility from land were visited by inflatable boat.

### Collection of explanatory variables

For each section, we collected a large number of variables, mostly related with disturbance, habitat characteristics and the geophysical characteristics of the coastline (Table 1).
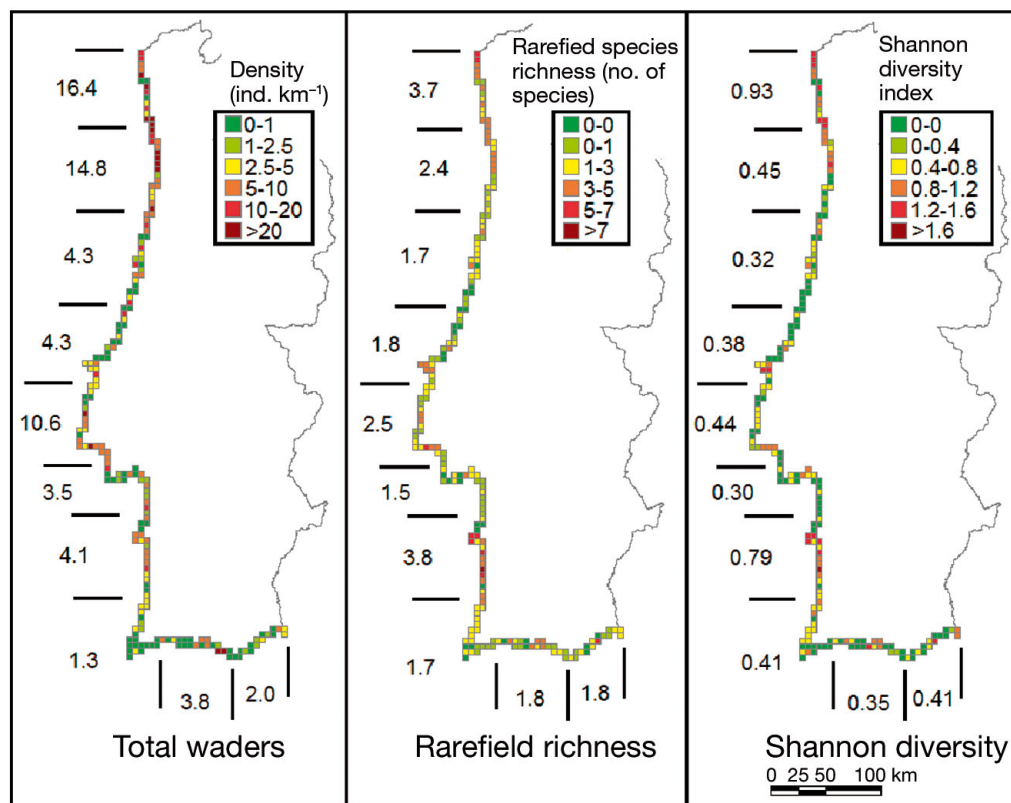


Fig. 1. Spatial distribution of total wader abundance, rarefied species richness and Shannon diversity index along the Portuguese non-estuarine coastline. We present the data for each 5 × 5 km Universal Transverse Mercator square and the averages for 10 sub-sections of the coast, each including roughly 20 squares

Table 1. Explanatory variables used in the analyses with indication of the type of variable, its average and standard deviation, the scale in which it varied and the source from where it was obtained. See 'Methods: Collection of explanatory variables' for description of variables

| Variable | Average ± SD | Type | Scale | Source |
|---|---|---|---|---|
| **Disturbance variables** | | | | |
| No. of people | 21 ± 35 | Continuous scale | Coast section | Collected in the field |
| No of dogs | 2 ± 4 | Continuous scale | Coast section | Collected in the field |
| Human density | 436 ± 716 km$^{-2}$ | Continuous scale | Township | INE (2011) |
| Proportion urbanized coast | 0.15 ± 0.18 | Continuous scale | Coast section | Google Earth |
| No. of peregrine falcons | 0.6 ± 1.0 pairs | Continuous scale | 10 × 10 km squares | Equipa Atlas (2008) |
| No. of fishing harbours | 0.2 ± 0.5 | Continuous scale | Coast section | Google Earth |
| **Habitat variables** | | | | |
| Proportion rocky coastline | 0.41 ± 0.35 | Continuous scale | Coast section | Google Earth |
| Width rocky intertidal | 9 ± 11 m | Continuous scale | Coast section | Google Earth |
| Width sandy intertidal | 43 ± 22 m | Continuous scale | Coast section | Google Earth |
| No. of river mouths (<10 m) | 0.5 ± 0.9 | Continuous scale | Coast section | Google Earth |
| No. of river mouths (10–100 m) | 0.2 ± 0.5 | Continuous scale | Coast section | Google Earth |
| No. of river mouths (>100 m) | 0.2 ± 0.4 | Continuous scale | Coast section | Google Earth |
| Presence of estuarine wetlands (<5 km) | | Presence/absence | Coast section | Google Earth |
| **Geophysical variables** | | | | |
| Distance to 10 m isobaths | 0.8 ± 0.7 km | Continuous scale | 1:150000 | Instituto Hidrográfico (1982) |
| Distance to 20 m isobaths | 2.4 ± 1.7 km | Continuous scale | 1:150000 | Instituto Hidrográfico (1982) |
| Distance to 30 m isobaths | 3.4 ± 2.3 km | Continuous scale | 1:150000 | Instituto Hidrográfico (1982) |
| Distance to 50 m isobaths | 7.8 ± 4.7 km | Continuous scale | 1:150000 | Instituto Hidrográfico (1982) |
| Wave energy | 23 ± 9 kW m$^{-1}$ | Continuous ordinal | 1:1000000 | Leandro (2010) |
| Geology | | Categorical nominal | 1:200000 | SGP (1992) |
| Orientation | | Categorical nominal | Coast section | Google Earth |
| Rainfall | 194 ± 56 mm | Continuous scale | Township | SNIRH (2012) |
| Minimum temperature | 7.8 ± 1.2°C | Continuous scale | Township | Instituto de Meteorologia (2012) |
| **Complex variables** | | | | |
| Substrate fragmentation | 1.3 ± 1.2 km$^{-1}$ | Continuous scale | Coast section | Google Earth |
| Substrate diversity | 0.49 ± 0.38 | Continuous scale | Coast section | Google Earth |
| Tortuosity | 1.5 ± 0.8 | Continuous scale | Coast section | Google Earth |

Each observer counted the number of people and unleashed dogs in the intertidal area during bird counts, as measures of direct human disturbance. The proportion of urbanized coastline was measured as the extent of the coast encompassed by urban perimeters, and data for human population density were obtained from national census data (INE 2011), both providing measures of overall human presence. The number of fishing harbours was counted from aerial imagery.

The presence and abundance of predators, especially large falcons, can influence wader distribution (van den Hout et al. 2008), so we obtained the number of peregrine falcon *Falco peregrinus* breeding pairs per section of the coast from the Portuguese Breeding Bird Atlas (Equipa Atlas 2008). Peregrine falcons in Portugal are largely sedentary and remain in their coastal territories year-round (Catry et al. 2010).

We used aerial photography to classify the coastline as rocky or sandy and calculated the proportion of coastline covered by each substrate type (including both natural and man-made areas). Since the 2 variables (rocky and sandy) are complementary, we only used the proportion of rocky coastline in the analyses. To measure the widths of the intertidal area, we used the most recent Google Earth coverage for which the full Portuguese coast was covered in the same day (30 October 2006) to minimize the biases of measuring images taken at different tidal levels. Of course, even photos from the same day may be taken at different times, but the fact that these measurements showed a strong correlation with intertidal widths estimated in the field in some coastal sections (r = 0.81, n = 34, p < 0.001) gives us confidence that this is a reliable method. In each section, we measured the intertidal width in 500 m inter-

vals along the coastline, measuring the distance between the sea and the high water mark, which was clearly visible as a darker band in the image. This provided an average of 14 measurements per section of the coast, which were classified into 2 groups: rocky intertidal and sandy intertidal.

The number of river or lagoon mouths was divided into 3 size classes: up to 10 m, between 10 and 100 m, and over 100 m in width. Since most wader species gather in estuarine wetlands during winter, we also determined if there were any major estuarine wetlands within 5 km of each section.

Waves are an important aspect of exposed oceanic coastlines such as the Portuguese coast. Coastal waves mainly result from offshore wind patterns and may differ among different parts of the coast. We obtained data on wave energy (in 9 classes, 0 to 45 kW m$^{-1}$) from a survey of the coast made by the Port and Marine Shipping Institute in 2003 (Leandro 2010). The bathymetric profile of the coast determines how waves dissipate their energy over the shore (Bird 1984) and may influence the availability of the intertidal area for birds. We evaluated the bathymetric profile by measuring the average distance of the coastline to the first 4 isobaths (10, 20, 30 and 50 m) from 1:150000 hydrographical charts (Instituto Hidrográfico 1982). For each section, we drew 4 lines perpendicular to the coast and measured the distance from the coastline (which in these charts is represented by the lowest recorded low tide) to each isobath, averaging the measurements for each section.

We also used 2 categorical variables, the orientation and the geology of the coast. Orientation is predominantly W or S along the Portuguese coast. Geology was classified into 8 main classes, following the 1:200 000 geological charts (SGP 1992): (1) sand dunes and beaches, (2) granites, (3) limestones and dolomites, (4) sandstones, (5) basalts, (6) schists and greywackes, (7) diabases and (8) calcarenites. Each section of the coast was classified into the geological class that covered the highest proportion of its coastline. Since the geology of the coast varies at a much broader scale than the size of our 5 × 5 km grid, the assigned geological class typically represented 100 % of the square, with the only exception being the grid squares located in transitions between different geological classes. Further analysis showed that in terms of their impact on wader distributions, these classes could be grouped into 3 main geological classes: sand dunes and beaches, sedimentary rocks (3, 4 and 8), and igneous and metamorphic rocks (2, 5, 6 and 7).

Two weather variables were used: average rainfall and average minimum temperature. We used the available data for December 2009 to February 2010, the period when >95 % of the bird surveys took place. The following winter (when the other surveys took place) was very similar in terms of average minimum temperature (7.2 ± 0.3 vs. 7.1 ± 0.3°C, n = 3 mo in each winter) and was only slightly less rainy (128.4 ± 39.5 vs. 83.3 ± 52.9 mm, n = 3 mo in each winter). Rainfall data were from SNIRH (2012), and temperature data were from Instituto de Meteorologia (2012).

Finally, we collected 3 complex variables (substrate fragmentation, substrate diversity and tortuosity of the coast) in an attempt to investigate how the overlying structure of the coast may influence waders. The first was measured as the number of transitions between rocky/sandy areas per kilometre of coastline. Substrate diversity was calculated as $1 - (R - S)^2$, where $R$ is the proportion of rocky coastline and $S$ is the proportion of sandy coastline in each section of the coast. Tortuosity was calculated as the total length of the coastline in a section divided by the linear distance between the 2 points where the coastline intercepts the edges of the coastal section.

## Statistical analysis

All counts were converted into kilometric abundances to account for the large differences in the length of the coastline between different sections of the coast (range 1130 to 17 550 m). We also calculated measures of species richness and diversity. For the first, we calculated the rarefied species richness, to allow an unbiased comparison between sections with different numbers of individuals (Hurlbert 1971), using a sample size of 50, which was roughly the average number of individuals per section. For diversity, the widely used Shannon diversity index was calculated to allow comparisons with the results of other studies.

All kilometric abundances were log-transformed [log $(x + 1)$] to reduce the skewness of the data. Also, we tested for collinearity between the explanatory variables. Some variables or groups of variables were highly correlated. The 4 variables related to human disturbance (human density, proportion of urbanized coast, number of people and number of unleashed dogs) were highly correlated and were thus aggregated in a principal component analysis (PCA). Principal component 1 (PC1) and principal component 2 (PC2) explained 80.9 % (PC1 = 56.8 %; PC2 = 24.1 %)

of the variation, with positive values of PC1 indicating decreasing levels of disturbance (loadings: human density, −0.62; urbanized coast, −0.73; people, −0.84; dogs, −0.80), while PC2 distinguishes the effect of direct disturbance by people and dogs and overall human presence, with positive values indicating higher direct disturbance and negative values indicating higher overall human presence (loadings: human density, −0.63; urbanized coast, −0.42; people, 0.39; dogs, 0.47).

The 4 measures of bathymetric profile were also highly correlated and aggregated in a PCA. In this case, PC1 and PC2 explained 91.8% (PC1 = 76.7%; PC2 = 15.1%) of the variation. We only found a significant effect of PC1 in the analysis, so PC2 will not be mentioned any further. Positive values of PC1 indicate a decreasing distance to all isobaths, thus corresponding to a more abrupt bathymetric profile (loadings: 10 m isobath, −0.78; 20 m isobath, −0.95; 30 m isobath, −0.95; 50 m isobath, −0.81).

The presence of estuarine wetlands within 5 km was highly correlated with the number of large river mouths (over 100 m), so we removed the variable from the analyses. All of the remaining variables showed low collinearity (r < 0.2) and were kept in our analyses. All independent variables used in our analysis were standardised to allow for comparisons between their coefficients.

We fitted the data using General Linear Models (GLMs), assuming a Gaussian error distribution, and selected the best models using the Akaike Information Criterion (AIC) through backwards stepwise selection. When the best-fitted models included the categorical variables of orientation and geology, we used Kruskal-Wallis and Mann-Whitney tests to compare the different groups.

The geography of the coast and the use of variables that vary on a larger scale than that of our coastal sections led to some level of spatial autocorrelation in the distribution of some variables. This could have an influence on the analyses, so to evaluate this problem, we tested for spatial autocorrelation in the residuals of GLMs using the Moran's $I$ statistic.

All statistical analyses were performed on R 2.14.2 (R Development Core Team 2012) and Statistica 8.0.

## RESULTS

Overall, 13 wader species were detected along the Portuguese non-estuarine coast. The most abundant species were sanderling (2897), ruddy turnstone (2191) and Kentish plover (581), which occurred in 30 to 60% of the coastal sections. Another 6 species were present in over 10% of the sections: whimbrel (21%), common ringed plover (15%), common sandpiper (15%), oystercatcher *Haematopus ostralegus* (13%), grey plover *Pluvialis squatarola* (12%) and dunlin *Calidris alpina* (10%). The remaining 4 species (purple sandpiper *Calidris maritima*, red knot *Calidris canutus*, bar-tailed godwit *Limosa lapponica* and golden plover *Pluvialis apricaria*) were found in less than 2% of the squares and were not used for analysis.

There were clear differences in the abundance of waders along the Portuguese non-estuarine coast. The highest abundances were found in the northern and central portions of the western coast, while the southern coast showed the lowest abundances (Fig. 1). Species richness was also high in the northern coast but achieved its highest values on the southwestern coast, while the central parts of the western coast and the southern coast had lower specific richness (Fig. 1). Diversity showed a similar pattern to species richness, with higher values on the northern and southwestern coast (Fig. 1).

### GLMs of wader abundance

A total of 15 explanatory variables were included in the final fitted models for specific abundance and total wader abundance. The models for the 3 most frequent species and for total wader abundance explained a relatively high proportion of the variation ($R^2 = 0.21 − 0.64$; Table 2), while the models for the less frequent species had a lower explanatory power ($R^2 = 0.09 − 0.17$; Table 3).

The 2 human disturbance variables were included in several of the final fitted models. The negative coefficients of PC1 indicate that most species are more abundant near areas of high human presence. The negative coefficients of PC2 suggest that within these areas, they tend to avoid direct disturbance in the form of people or unleashed dogs. The number of peregrine falcon breeding pairs had a negative effect on the abundance of ruddy turnstone and total wader abundance, also being included in the final fit for whimbrel abundance. The number of fishing harbours had a negative effect on the abundance of sanderling and Kentish plover but a positive effect on the abundance of dunlin.

In terms of habitat variables, the number of large river mouths had an effect on the abundance of Kentish plover and oystercatcher and was also included in the final fits for whimbrel, grey plover and dunlin.

Table 2. Coefficients (±SE) of the standardized variables included in the final fitted General Linear Models for the 3 most frequent species (occurring in over 30% of coastal sections), total wader abundance, rarefied species richness and Shannon diversity. Parentheses: variables that were included in the final model, but for which the effect was not significantly different from 0. For the categorical variables (Orientation and Geology), we simply indicate if the variable was included in the final fit. We also present the $R^2$ of each fit

| Variable | Sanderling | Ruddy turnstone | Kentish plover | Total waders | Rarefied richness | Shannon diversity |
|---|---|---|---|---|---|---|
| Human disturbance PC1 | −0.38 ± 0.07 | −0.36 ± 0.07 | | −0.29 ± 0.08 | | |
| Human disturbance PC2 | (−0.14 ± 0.11) | −0.36 ± 0.06 | −0.17 ± 0.08 | −0.19 ± 0.07 | | |
| Peregrine falcons | | −0.18 ± 0.07 | | −0.15 ± 0.07 | (−0.16 ± 0.09) | |
| Harbours | −0.17 ± 0.07 | | −0.25 ± 0.07 | | | |
| Proportion rocky coastline | −0.25 ± 0.11 | 0.48 ± 0.09 | −0.18 ± 0.09 | | 0.31 ± 0.12 | |
| Width rocky intertidal | | 0.23 ± 0.07 | | 0.19 ± 0.7 | | 0.19 ± 0.09 |
| Width sandy intertidal | | | (−0.14 ± 0.08) | | | (−0.13 ± 0.07) |
| River mouths (>100 m) | | | 0.26 ± 0.07 | | (0.13 ± 0.07) | 0.24 ± 0.08 |
| Bathymetry PC1 | | (−0.11 ± 0.07) | | (−0.12 ± 0.08) | | |
| Orientation | | Yes | | Yes | | |
| Geology | Yes | Yes | | | Yes | Yes |
| Minimum temperature | −0.18 ± 0.08 | | −0.30 ± 0.08 | −0.19 ± 0.09 | −0.18 ± 0.07 | −0.21 ± 0.07 |
| Subtrate fragmentation | | | −0.28 ± 0.11 | | | |
| Substrate diversity | | | 0.48 ± 0.12 | 0.26 ± 0.06 | 0.36 ± 0.09 | 0.41 ± 0.09 |
| $R^2$ | 0.34 | 0.64 | 0.21 | 0.44 | 0.31 | 0.32 |

Table 3. Coefficients (±SE) of the standardized variables included in the final fitted General Linear Models for the remaining species occurring in over 10% of coastal sections. Parentheses: variables that were included in the final model but for which the effect was not significantly different from 0. We also present the $R^2$ of each fit

| Variable | Whimbrel | Ringed plover | Common sandpiper | Oystercatcher | Grey plover | Dunlin |
|---|---|---|---|---|---|---|
| Peregrine falcons | (−0.15 ± 0.10) | | | | | |
| Harbours | (−0.14 ± 0.09) | (−0.13 ± 0.08) | | (−0.10 ± 0.08) | | 0.27 ± 0.08 |
| Proportion rocky coastline | 0.40 ± 0.11 | | 0.35 ± 0.09 | | | |
| Width rocky intertidal | (0.15 ± 0.08) | (0.14 ± 0.09) | (−0.13 ± 0.08) | 0.23 ± 0.07 | 0.31 ± 0.07 | |
| River mouths (>100 m) | (0.13 ± 0.08) | | | 0.23 ± 0.08 | (0.13 ± 0.08) | (0.10 ± 0.08) |
| Bathymetry PC1 | | | (−0.13 ± 0.09) | 0.19 ± 0.08 | | |
| Wave energy | | | | (0.13 ± 0.07) | | (0.16 ± 0.09) |
| Rainfall | | | | 0.18 ± 0.06 | | 0.21 ± 0.07 |
| Minimum temperature | | −0.26 ± 0.07 | | | | −0.19 ± 0.08 |
| Substrate diversity | | 0.21 ± 0.09 | | | | |
| $R^2$ | 0.17 | 0.15 | 0.09 | 0.17 | 0.12 | 0.16 |

The proportion of rocky shoreline had a negative effect on sanderling and Kentish plover abundance but a positive effect on the abundance of ruddy turnstone, whimbrel and common sandpiper. The width of rocky intertidal areas had a positive effect on total wader abundance and on the abundance of several species.

The PC1 orthogonal of the bathymetry variables had a negative effect on the abundance of ruddy turnstone and a positive effect on the abundance of oystercatcher. This suggests that ruddy turnstone is more abundant in coastal sections with a more gradual bathymetry, while oystercatcher is more abundant in areas of more abrupt bathymetry. Average rainfall had a positive effect on the abundance of

oystercatcher and dunlin, while average minimum temperature had a negative effect on most species.

The orientation of the coast had an effect on total wader abundance and on the abundance of ruddy turnstone. In both cases, the average abundance was significantly higher in predominantly W-oriented sections (Mann-Whitney tests; ruddy turnstone: $Z = 3.19$, $p < 0.01$, median west-oriented = 0.30 [0 − 27.5], n = 123, median south-oriented = 0.00 [0 − 2.62], n = 23; total waders: $Z = 3.89$, $p < 0.01$, median west-oriented = 4.36 [0 − 77.8], n = 123, median south-oriented = 0.57 [0 − 29.5], n = 23). The geology of the coast was included in the final models for sanderling and ruddy turnstone. In both cases, there were significant differences between the 3 main

geological classes (Kruskal-Wallis tests; sanderling: $H_{(2,156)}$ = 19.3, p < 0.001; ruddy turnstone: $H_{(2,156)}$ = 26.1, p < 0.001), but post hoc tests revealed that these results simply reflect a difference between sandy and rocky areas, with the sanderlings showing higher densities in sandy areas and ruddy turnstones showing higher densities in rocky areas, regardless of their underlying geology.

Two complex variables were included in the final fits for wader abundance. Substrate diversity had a positive effect on total wader abundance and on the abundance of Kentish and ringed plovers. Substrate fragmentation had a negative effect on the abundance of Kentish plovers.

In 2 cases, the models for oystercatcher (Moran's $I$ observed: 0.0547, expected: −0.0065, p < 0.001) and common sandpiper (Moran's $I$ observed: 0.0846, expected: −0.0065, p < 0.001), the residuals showed significant spatial autocorrelation. In all other cases, we found no evidence for spatial autocorrelation in the residuals of the models (p = 0.12 − 0.49).

### GLMs of species richness and diversity

Six explanatory variables were included in each of the final fitted models for the Shannon diversity index and rarefied species richness (Table 2). The human disturbance variables were not included in these models, while the number of peregrine falcon breeding pairs was included in one of the models, but their effect was not significantly different from 0.

The number of large river mouths had a positive effect on both richness and Shannon diversity, but this effect was only significantly different from 0 for Shannon diversity. The proportion of rocky coastline had a positive effect on species richness. The width of the intertidal was included in the model for Shannon diversity, but the intertidal width on rocky areas had a positive effect while the intertidal width on sandy areas had a negative effect. The average minimum temperature had a negative effect on both richness and Shannon diversity.

The geology of the coast was included in both models. In both cases, there were significant differences between the 3 main groups (richness: $H_{(2,156)}$ = 14.0, p < 0.001; Shannon diversity: $H_{(2,156)}$ = 12.5, p < 0.01). Post hoc tests indicated that both richness and Shannon diversity are significantly higher in areas dominated by igneous and metamorphic rocks, while areas dominated by sedimentary rocks and sandy beaches have similar values (Fig. 2).
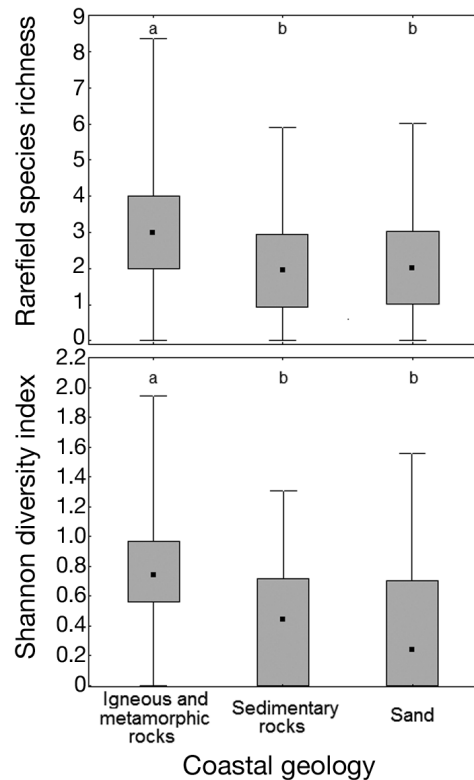


Fig. 2. Differences in rarefied species richness and Shannon diversity index between the 3 main coastal geology classes (hard rocks: n = 33; soft rocks: n = 57; sand: n = 66). Black dot: median; grey box: inter-quartile range; whiskers: minimum and maximum. Different letters in the graph indicate significant differences in post hoc tests

In both the model for rarefied species richness (Moran's $I$ observed: −0.0099, expected: −0.0065, p = 0.84) and for Shannon diversity index (Moran's $I$ observed: −0.0095, expected: −0.0065, p = 0.87), the residuals were not spatially autocorrelated.

## DISCUSSION

### Variables explaining wader abundance and diversity in non-estuarine coastal areas

The distribution of waders in non-estuarine intertidal areas seems to be explained by variables related to disturbance, habitat characteristics and the geophysical characteristics of the coast. Variables such as disturbance by humans and bird predators and sediment characteristics have also been shown to influence the distribution of waders in estuarine areas (e.g. Mouritsen & Jensen 1992, Gill et al. 2001, van den Hout et al. 2008), but other variables such as intertidal width, proportion of rocky shoreline (Sum-

mers et al. 2002), geology and ocean bathymetry near the coast appear to be of particular importance in non-estuarine areas. Also, since non-estuarine coastal areas cover much wider stretches of coastline, weather variables such as temperature and rainfall, which vary at larger scales, become important (Rehfisch et al. 2004).

Direct disturbance by humans and peregrine falcons negatively affected the numbers of these birds, while overall human presence, the availability of rocky intertidal areas and the presence of nearby estuarine wetlands favoured higher wader densities. The average minimum temperature and the diversity of substrates on a coastal section also influenced the abundance of waders and, together with coastal geology, seem to be important factors structuring wader communities in non-estuarine areas, influencing species richness and diversity.

The models for total wader abundance, richness, diversity and most abundant species explained a relatively high proportion of the variation in our data, giving us confidence that the described patterns reflect real relationships between the dependent and independent variables. However, we must be more cautious when interpreting the results of the models for the least abundant species, which had a relatively low explanatory power. Still, the consistency in the effects of several variables across multiple species seems to confirm that even these weaker models may provide some valid insights into the factors structuring spatial patterns of wader abundance. The lack of spatial autocorrelation in the residuals of most models suggests that the patterns we found are not caused by statistical artefacts or the skewness of the data.

Wader abundances were higher in areas of strong human presence, with high human population densities and a larger proportion of urbanized coast. Human presence can lead to organic enrichment due to sewage discharge, which can locally increase productivity, ultimately favouring top predators such as waders (van Impe 1985, Burton et al. 2002). This may also reflect an increase in the availability of man-made intertidal habitats, such as piers, sea walls and artificial sandy beaches, which are readily used by species such as ruddy turnstone, purple sandpiper or sanderling (Dierschke 1993). Also, the original human settlements were more likely to be sited in the richer areas along the coast, where fishing was more profitable, and where waders were probably more abundant, which may still influence this present-day correlation. Since most peregrine falcon pairs along the Portuguese coast are concentrated in areas away from large human settlements (Equipa Atlas 2008),

human presence may also favour waders by reducing the risk of predation, but the analyses suggest that the 2 variables have independent effects on wader distributions. The recreational use of intertidal areas, here evaluated by the presence of people and unleashed dogs, had a negative influence on wader abundance, similar to what was previously shown elsewhere (Pfister et al. 1992, Gill et al. 2001).

The presence of large falcons can have a strong impact on waders, which either avoid areas where falcons are present (Lank et al. 2003, Ydenberg et al. 2007) or change their behaviour to reduce the risk of being attacked (Dekker et al. 2011). The peregrine falcon is the only large falcon commonly found along the Portuguese coast (Equipa Atlas 2008), and our data indicate that its presence reduced total wader abundance and may also reduce species richness, suggesting that these predators limit the availability of coastal habitats for some waders, namely ruddy turnstone. This effect could reflect an avoidance of areas with higher risk of mortality or a reduction of habitat quality through non-lethal effects (Cresswell 2008).

Substrate type has long been known to influence intertidal communities. Not surprisingly, sanderling was negatively affected by the proportion of rocky shoreline and occurred in higher densities in sandy areas, as was expected for a species associated with sandy shores (Clark et al. 1993, Summers et al. 2002). Ruddy turnstone, whimbrel and common sandpiper were positively affected by the proportion of rocky coastline, and the first 2 showed significantly higher densities in rocky areas. While the first is a rocky shore specialist (Summers et al. 2002), the other 2 species use a wider range of substrates, namely softer substrates that were not available along the non-estuarine coastline, so this association was unexpected. Interestingly, in rocky areas, the width of the intertidal area was positively correlated with wader abundance, similar to what has been described in previous studies (Summers et al. 2002), but in sandy areas this effect was absent or even negative. This difference possibly relates to the fact that species in rocky areas tend to use all of the available intertidal habitat, while the 2 species more associated with sandy areas, sanderling and Kentish plover, use only a small portion of the intertidal area. Sanderlings feed along the surf line, while Kentish plovers mainly use supra-tidal sand dunes and wrack deposits along the high water mark (Beeler 2009), in neither case benefiting from a wider intertidal area. This difference may relate to the fact that invertebrates in sandy flats are more mobile and bury deeply to avoid desiccation (Brown &

McLachlan 1990), becoming unavailable for bird predators, while in rocky intertidal areas many organisms are sessile, and small pools and rock crevices provide better protection from desiccation for mobile species, which remain available for birds (Dumas & Witman 1993).

The presence of large river mouths was positively associated with the abundance of several species, as well as included in the models for species richness and diversity. This variable was highly correlated with the presence of estuarine wetlands within 5 km of the coast. Waders can cover this distance every low tide in search of foraging areas (Dias et al. 2006), so individuals in these coastal sections can, at least in theory, access the nearby estuarine habitats, which could explain the higher abundance of common estuarine species such as oystercatcher, grey plover and dunlin in these areas. Also, the presence of large river mouths should reflect a large input of organic matter, locally increasing productivity and, consequently, food availability for predators (Jickells 1998).

Although included in several final models, the relationship between the bathymetry of the coast and wader abundance was not clear. Ruddy turnstone seems to favour more gentle coastal profiles, while oystercatchers were more abundant in more abrupt areas. This could relate to wave exposure, as in fact oystercatchers were also weakly associated with areas of higher wave energy. Waves may limit food availability near the surf (Nordstrom et al. 2006), but higher wave exposure may create more feeding opportunities above the high water mark, due to the creation of pools in the splash zone that harbour intertidal invertebrates in areas otherwise unavailable for these species (Raffaelli & Hawkins 1996).

We used 2 weather variables in our analysis: average rainfall and average minimum temperature. The first only had a positive effect on the abundance of 2 of the least abundant species, while the second had a consistently negative impact on wader abundance, richness and diversity. These results indicate a weak response to rainfall and a general preference for areas of lower temperature, which contradict the patterns observed in the UK, where average rainfall has a negative impact on the abundance of several coastal waders, while minimum temperature has opposite effects on different species (Rehfisch et al. 2004). Increased rainfall may limit invertebrate availability (Pienkowski 1983), but it may also reduce the risk of desiccation for intertidal invertebrates, which is likely more important in Portugal, where winters are much warmer and drier than in the UK. Likewise,

low temperatures are not likely to be a problem for waders in the mild conditions found along the Portuguese coast but may reduce the risk of desiccation for invertebrates, which can thus remain exposed and available to predators for longer periods.

The geology of the coast seems to have an effect on wader communities, influencing both species richness and diversity. Although geological factors had already been suggested to influence bird distributions almost 80 yr ago (Kelly 1935), no studies to our knowledge relate the structure of intertidal bird assemblages with the underlying geological characteristics of the coast. We found that the wader community in coastal sections dominated by igneous and metamorphic rocks was richer and more diverse than in areas of sand or sedimentary rocks. Rock type can influence the abundance of macroinvertebrates (Raimondi 1988, Herbert & Hawkins 2006), so the former could mediate the impact of the latter on waders. However, the fact that rock type influences species richness and diversity, but not abundance, seems to suggest that the effect of rock type is functioning at the community level. The exact mechanism by which different rocks influence wader communities is not yet clear, and there are no previous studies on the topic from which to infer such a mechanism. However, we note that sedimentary rocks tend to be softer than igneous or metamorphic rocks (Bogs 2009). Soft rocks such as limestones and sandstones are easily weathered into sand or more delicate formations, whereas harder rocks such as granite, basalt or schist are more rugged, with plenty of crevices and small pools. In this way, igneous and metamorphic rocks may provide a wider range of microhabitats for intertidal invertebrates (Barry & Dayton 1991) and possibly increase the diversity of available prey items, thus increasing the range of foraging opportunities for waders and possibly allowing the co-occurrence of a larger number of predator bird species. Future detailed studies are required to determine how the relationship between wader distribution and coastal geology functions.

### Implications for the management of non-estuarine coastal areas

Many wader species are currently declining worldwide, in part due to habitat loss and degradation within their wintering range. This has prompted the protection and management of many estuarine wetlands, but the importance of non-estuarine coasts for wader conservation is poorly known. Detailed moni-

toring data are available for only a few countries (Burton et al. 2008), so in most regions the importance of non-estuarine coastal areas for waders is unclear, and it is impossible to evaluate where one should focus conservation and management efforts to maintain these important habitats.

Based on our results, and on the few previous studies on this subject, we were able to identify the characteristics of coastal areas likely to favour wader populations, which may help determine where conservation efforts should be focused. Clearly, areas with a wide intertidal area are particularly important for species that favour rocky substrates, and high substrate diversity allows for higher species richness and diversity, suggesting that coasts with a mixture of rocky and sandy areas can support more wader species. Areas near large rivers mouths are also particularly favourable for wader communities. Overall human presence is not necessarily a negative factor, as long as direct disturbance is kept to a minimum, while the influence of weather variables is likely to vary between different geographic areas.

We found that the geology of the coast may also influence wader communities. Areas with igneous and metamorphic rocks, such as granites, schists, basalts and diabases, support a richer and more diverse assemblage of species, and so may deserve higher priority when planning the conservation of non-estuarine coastal areas.

Although our results are based on a sample of over 1000 km of coastline, this was still a relatively localized effort. Consequently, we cannot be certain of how these conclusions extrapolate for coastlines in other geographic areas. Since the Portuguese coast is rather diverse, our sampling covered many environmental characteristics found in other coastlines. Therefore, we believe the patterns found here are likely similar to those found in other coastlines with similar meteorological, oceanographic and geologic characteristics, and where the wader community has a similar composition. Only future studies will determine the extent to which these patterns will hold for coastal areas with different characteristics.

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